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ECOLOGICAL COMPARISON OF SYMPATRIC POPULATIONS OF SAND LIZARDS (*COPHOSAURUS TEXANUS* AND *CALLISAURUS DRACONOIDES*)

Donald D. Smith^{1,2}, Philip A. Medica^{1,3}, and Sherburn R. Sanborn⁴

ABSTRACT.—Sympatric populations of *Cophosaurus texanus* and *Callisaurus draconoides* were periodically sampled from March 1973 through April 1974 at Burro Creek, Mohave County, Arizona. *Callisaurus* were also sampled at Rock Valley, Nye County, Nevada. Sex ratios were skewed in favor of males in the adult *Cophosaurus* but were equal in both adult populations of *Callisaurus*. Both species became sexually mature as yearlings. Mean clutch sizes were 3.55 (± 0.83) for *Cophosaurus*, and 4.25 (± 1.08) and 5.07 (± 1.33) for *Callisaurus* at Burro Creek and Rock Valley respectively. Evidence of multiple clutches was exhibited by both species. Egg weight/body weight ratios for both species and clutch weight/body weight ratios for *Cophosaurus* were notably smaller than previously reported.

At Burro Creek both species were highly insectivorous, with orthopterans comprising the largest food group of each. Niche overlap for food was high at the ordinal level, but at the familial level it is apparent that *Callisaurus* probably fed in the more xeric areas of the riparian habitat.

No differences were found in the temperature responses of these two lizards. However, minor temporal separations and substantial spatial partitioning were observed. *Callisaurus* preferred sandy open areas, while *Cophosaurus* preferred the presence of some rocks and boulders.

Ecological studies of *Callisaurus draconoides* have been conducted by Kay et al. (1970), Pianka and Parker (1972), Tanner and Krogh (1975), and Vitt and Ohmart (1977). Studies of *Cophosaurus texanus* have been done by Johnson (1960), Ballinger et al. (1972), Shrank and Ballinger (1973), Engeling (1972), and Howland (1984). Clarke (1965) studied the ethology of both of these lizards as well as that of *Holbrookia*. Prior to our field work, no comparative ecological study had been done of sympatric populations of *Callisaurus draconoides* and *Cophosaurus texanus*. These two sand lizards are recognized as being closely related (Peters 1951, Clarke 1965) and exhibit geographic distributions that are usually mutually exclusive. It is hoped that this study will provide insights into

their descriptive ecological characteristics and some of the interrelationships of these two populations.

In the spring of 1966, P. A. Medica collected a single specimen of *Cophosaurus texanus* near Burro Creek, 32 km S of Wikieup, Mohave County, Arizona. In May 1970, D. D. Smith discovered *C. texanus* near the same locality to be sympatric with *Callisaurus draconoides*. This area is described in Stebbins (1966) as a disjunct locality in the distribution of *Cophosaurus*. Another pair of saurian species not often found to be sympatric were also present at the study site, *Uta stansburiana* and *Urosaurus ornatus*. Other species of reptiles and amphibians observed at the study locality include *Cnemidophorus tigris*, *Sauromalus obesus*, *Sceloporus magis*-

¹University of California, Laboratory of Biomedical and Environmental Sciences, 900 Veteran Avenue, Los Angeles, California 90024.

²Present address: Department of Pathology, University of Kansas Medical Center, 39th Street and Rainbow Boulevard, Kansas City, Kansas 66103.

³Present address: Natural History Museum of Los Angeles County, Section of Herpetology, 900 Exposition Boulevard, Los Angeles, California 90007.

⁴Department of Biology, California State University, Long Beach, California 90840. Present address: 13615 Arnold Drive, Glen Ellen, California 95442.

ter, *Crotalus mitchelli*, *Kinosternon sonorense*, *Bufo microscaphus*, and *Hyla arenicolor*. Additional noteworthy locality records have been recorded for *Thamnophis cyrtopsis* (Smith and Medica 1973), *Eumeces gilberti* (Medica and Vitt 1974), and *Masticophis bilineatus* (Medica and Maza 1974).

METHODS

Between 3 March 1973 and 7 April 1974 nine weekend field trips were taken to Burro Creek (15 km W of Bagdad), Mohave County, Arizona. Field work normally began about 0700 hours (hr) and continued until approximately 1400 hr when most lizard activity had ceased. Then in the evening we sampled lizards again between 1730 hr and sunset. Lizards were collected along either side of Burro Creek and from the water's edge sometimes up the arroyos and onto the surrounding bajadas. Lizards were collected by noosing or by shooting with BB guns or .22-caliber revolvers loaded with #12 shot cartridges.

Each time a lizard was secured, the following data were recorded: cloacal temperature, air temperature at about 2 cm, and soil surface temperature using a Schultheis quick-reading thermometer 20–70 C. The habitat type, soil type, and lizard's activity were also recorded. The animals were then frozen with dry ice and transported to the laboratory for autopsy. From the Burro Creek locality 116 *Cophosaurus texanus* and 132 *Callisaurus draconoides* were removed for analysis. In addition, during the summer of 1973, a parallel sample of 91 *C. draconoides* was collected from Rock Valley, Nye County, Nevada (322 km NW of Burro Creek), to be analyzed similarly to those from Burro Creek for information on reproduction. This was done in an effort to gain insight into latitudinal variation in this species during the same season and to obtain further baseline data for comparison with the well-studied population of Frenchman Flat reported by Tanner and Krogh (1975). All specimens have been deposited at the Los Angeles County Museum of Natural History, Section of Herpetology.

In the laboratory, snout-vent (s-v) and tail lengths were measured to the nearest mm, weights were recorded to the nearest mg, and the lizards were autopsied to determine reproductive condition. Ovaries and oviducal

eggs were weighed, and clutch size was determined by counting yolked follicles ≥ 3 mm in diameter, oviducal eggs, and/or corpora lutea. In males the testes were weighed and their length and width measured. The amount of fat present and the weight of stomach contents of both sexes were also recorded. Stomach volume was determined by displacement of water in a graduated centrifuge tube and measured to the nearest 0.01 ml as described by Sanborn (1972). The stomach contents were separated and identified to family whenever possible, and their volume estimated.

RESULTS AND DISCUSSION

Reproduction

SEX RATIOS.—Sex ratios of *Cophosaurus* were skewed in favor of males in individuals ≥ 55 mm s-v, at 63:40, while in smaller individuals sexes occurred equally at 7:6. Sex ratios of adult *Callisaurus* at both Burro Creek and Rock Valley were close to one-to-one with male-to-female ratios of 53:50 and 42:40 for individuals ≥ 55 mm at Burro Creek and ≥ 60 mm at Rock Valley respectively. In contrast, sex ratios of younger *Callisaurus* from both localities were skewed in favor of females with sex ratios of 12:17 and 3:6 for Burro Creek and Rock Valley respectively.

Engeling (1972) concluded sex ratios of a population of marked *Cophosaurus* were equal. The disparity observed by us may be due to sampling error. Since male *Cophosaurus* often patrol, display, and observe from points of prominence, they would consistently be the most obvious and therefore the most commonly collected of the two sexes. The males are also larger and therefore easier to see. These arguments would also seemingly be true for *Callisaurus*, except that points of prominence are less common in the habitats most preferred by them. If it is true, however, it would agree with findings for the smaller-sized group with females being more common. If the females truly are more abundant in this species, the causes are unknown.

AGE AT MATURITY.—At Burro Creek during June and July no female *Cophosaurus* was found below the minimum reproductive size of 55 mm s-v. Only one *Callisaurus* was found below that s-v length, and it was a 52-mm female found on 1 June 1973. Similarly, no male *Cophosaurus* was found in June or July

below the length of 55 mm s-v, and the smallest weight of testes was 0.043 g. In contrast, three *Callisaurus* from Burro Creek in early June were found to measure ≤ 55 mm, had testes weights of 0.013, 0.002, and 0.001 g, and were probably not yet reproductive. Similarly sized male *Callisaurus* were not found in late June or July.

At Rock Valley no female *Callisaurus* was collected below 60 mm s-v in the months of June or July. However, two females < 55 mm collected in late May were not yet reproductive with ovarian weights of only 2 mg each. During June and July only one < 60 mm *Callisaurus* male was collected. It was collected on 8 June, measured 56 mm s-v, and had a testes weight of only 2 mg. Engeling (1972), Ballinger et al. (1972), Howland (1984), Pianka and Parker (1972), and Tanner and Krogh (1975) agree that most sand lizards become reproductive as yearlings.

FEMALE REPRODUCTIVE CYCLE.—The first evidence of follicular development at Burro Creek in 1973 was exhibited by *Callisaurus* that contained yolked follicles 2 to 7 mm in diameter on 28 April. Unfortunately, comparable samples of *Cophosaurus* could not be obtained at this sampling period. By 1 June adequate populations of both *Callisaurus* and *Cophosaurus* were located in sympatry, and series of 10 and 13 respectively were collected. Reproductive condition of *Cophosaurus* varied from small yolked follicles 3–5 mm in lizards < 60 mm s-v to oviducal eggs in females > 60 mm s-v. *Callisaurus* < 60 mm were usually determined to be prereproductive, and females > 60 mm s-v contained enlarged yolked follicles 3–9 mm in length or oviducal eggs. The reproductive season for both species apparently began by early May and was over in August. *Callisaurus* from Rock Valley probably ceased reproductive activities two to three weeks earlier than those at Burro Creek.

Ballinger et al. (1972) found follicles in *Cophosaurus* from 8 April through 9 August and oviducal eggs from 27 April through 9 August. Engeling (1972) concluded that their reproductive season was from March through August. Howland (1984) stated that oviposition extended from mid-May to late August. In *Callisaurus*, Pianka and Parker (1972) found yolked follicles from April through September. Vitt and Ohmart (1977) found oviducal

TABLE 1. Mean clutch size for various size groups of *Cophosaurus texanus* and *Callisaurus draconoides*, according to their availability.

Snout-vent length, mm	\bar{x}	Range	N
<i>Cophosaurus texanus</i> (Burro Creek)			
55–57	3.20 (± 0.45)	3–4	5
58–60	3.57 (± 0.79)	3–5	7
61–63	3.54 (± 0.88)	2–5	13
64+	4.00 (± 1.15)	3–5	4
All sizes	3.55 (± 0.83)	2–5	29
<i>Callisaurus draconoides</i> (Burro Creek)			
55–59	3.00	3	1
60–64	3.50 (± 0.58)	3–4	4
65–69	4.43 (± 1.09)	2–6	14
70–74	4.44 (± 1.13)	2–6	9
All sizes	4.25 (± 1.08)	2–6	28
<i>Callisaurus draconoides</i> (Rock Valley)			
65–69	4.00 (± 1.15)	3–5	4
70–74	4.82 (± 0.98)	3–6	11
75–79	5.22 (± 1.30)	3–7	9
80+	6.20 (± 1.64)	4–8	5
All sizes	5.07 (± 1.33)	3–8	29

cal eggs from May through August with vitellogenesis beginning by mid-April. And Tanner and Krogh (1975) found follicles and oviducal eggs from late May into July, with most seen in June.

Table 1 shows the mean clutch size for various size groups of sand lizards. Mean clutch sizes for all size groups are 3.55 (± 0.83) for *Cophosaurus* and 4.25 (± 1.08) and 5.07 (± 1.33) for *Callisaurus* at Burro Creek and Rock Valley respectively. There is a marked trend of an increase in clutch size with an increase in s-v length in both populations of *Callisaurus*, but this trend is not apparent in *Cophosaurus*. One record of a 69-mm *Callisaurus* collected on 8 September at Burro Creek with one 4-mm yolked follicle was deleted from this table, as it was not representative of the rest of the September sample and was the only record of a single-egged clutch. It is not known whether this ovum would have been deposited or resorbed.

The smallest *Cophosaurus* female found to be reproductive was 55 mm s-v with three yolked ovarian follicles 5 mm in diameter. The smallest reproductive *Callisaurus* from Burro Creek measured 58 mm s-v and contained three 7-mm follicles, while the smallest reproductive female from Rock Valley measured 65 mm s-v and had three oviducal eggs 17 mm long. Ballinger et al. (1972) and Engeling

TABLE 2. Clutch size and fat body weights (g) for female sand lizards ≥ 55 mm s-v. Date is mean date of collection.

Day and month	s-v range in mm (mean)	\bar{x} clutch size	Range	N repro/ N examined	\bar{x} fat body weight (S. D.)
<i>Cophosaurus</i> (Burro Creek)					
28 Apr	—	—	—	—	—
1 Jun	56-64(60.5)	3.55(± 0.69)	3-5	10/13	.068($\pm .067$)
23 Jun	55-64(60.3)	3.50(± 1.07)	2-5	8/9	.056($\pm .041$)
21 Jul	59-64(61.3)	3.60(± 0.84)	3-5	9/9	.014($\pm .018$)
8 Sep	—	—	—	0/5	.038($\pm .031$)
6 Apr	—	—	—	0/3	.073($\pm .059$)
<i>Callisaurus</i> (Burro Creek)					
10 Mar	—	—	—	0/4	.033($\pm .066$)
7 Apr	—	—	—	0/5	.052($\pm .056$)
28 Apr	67-70(68.8)	4.80(± 0.84)	4-6	5/7	.161($\pm .105$)
1 Jun	58-70(65.7)	4.29(± 1.11)	3-6	6/9	.047($\pm .067$)
23 Jun	60-70(65.0)	3.83(± 0.41)	3-4	6/8	.073($\pm .057$)
21 Jul	65-75(70.8)	4.20(± 1.40)	2-6	9/9	.023($\pm .038$)
8 Sep	—	—	—	0/6	.069($\pm .046$)
6 Apr	—	—	—	0/2	.161($\pm .099$)
<i>Callisaurus</i> (Rock Valley)					
2 May	72-82(77.0)	5.50(± 2.12)	4-7	2/5	.153($\pm .115$)
31 May	71-84(77.3)	6.25(± 1.04)	5-8	6/7	.191($\pm .100$)
8 Jul	65-82(72.9)	4.73(± 1.01)	3-6	11/13	.197($\pm .223$)
25 Jul	67-79(72.5)	4.25(± 1.16)	3-6	8/12	.227($\pm .267$)
13 Sep	—	—	—	0/1	.457

TABLE 3. Ranges of sizes of hatchling sand lizards found in September at Burro Creek, Mohave County, Arizona.

Species	Sex	Snout-vent length, mm	Weight, g
<i>Cophosaurus</i>	females	38-45	1.5-3.0
<i>Cophosaurus</i>	males	38-50	1.5-3.6
<i>Callisaurus</i>	females	30-46	0.7-3.3
<i>Callisaurus</i>	males	40-55	1.8-4.9

(1972) both found *Cophosaurus* to become reproductively mature at about 50 mm s-v, and Howland (1984) found them to mature between 52 and 55 mm s-v. Kay et al. (1970) found *Callisaurus* to become reproductive at 65 mm, Pianka and Parker (1972) recorded the smallest at 63 mm, and Tanner and Krogh (1975) found oviducal eggs in females as small as 66 and 67 mm s-v.

The mean clutch size of *Cophosaurus* has been variously reported at 2.8 (Hulse 1973), 3.1 (Howland 1984), 4.0 (Parker 1973), 4.6 (Vitt 1977), 5.0 (Johnson 1960), and 6.0-6.1 (Ballinger et al. 1972, Engeling 1972); and the pattern appears nonclinal and irregular as described by Fitch (1985). The mean clutch size of *Callisaurus* has been recorded at 4.4 (Pianka and Parker 1972), 4.5 (Vitt 1977, Tanner and Krogh 1975), and 4.6 (Vitt and Ohmart 1977), being apparently rather consistent

throughout its range. The mean of 4.25 eggs per clutch recorded at Burro Creek then is a reported low associated with range periphery and the mean of 5.07 at Rock Valley a reported high probably associated with a short-term consideration of high precipitation, as with the increased fecundity found in *Uta* from the same location during that same year (Medica and Turner 1976).

Table 2 shows mean clutch size, number of animals found to be reproductive, and \bar{x} fat body weights of female lizards sampled at various intervals. There was a trend for *Callisaurus* from Rock Valley to exhibit reduced fecundity through the breeding season. This trend was not as apparent for *Cophosaurus* and *Callisaurus* from Burro Creek. Peak periods of reproduction were in late July for both Burro Creek populations, while the *Callisaurus* from Rock Valley peaked in early July. Minimum mean fat body sizes were recorded for both *Cophosaurus* and *Callisaurus* at Burro Creek in the month of July, while the largest were recorded for both in the month of April. *Callisaurus* from Rock Valley maintained large fat bodies throughout the sampling period, probably due to unusually large amounts of precipitation presumably resulting in large quantities of food production during that year (Medica and Turner 1976). Vitt

TABLE 4. Reproductive data of *Cophosaurus* and *Callisaurus* based solely upon females carrying oviducal eggs. All mean values \pm one standard deviation.

	<i>Cophosaurus</i>	<i>Callisaurus</i>	
		Burro Creek	Rock Valley
Number of females	12	6	10
\bar{x} s-v length, mm	61.33 \pm 2.02	67.0 \pm 3.85	72.7 \pm 4.97
\bar{x} weight, g	8.169 \pm 1.218	10.422 \pm 1.405	13.375 \pm 3.860
\bar{x} clutch size	4.08 \pm 0.79	4.50 \pm 1.05	4.20 \pm 1.48
\bar{x} weight of clutch, g	1.270 \pm 0.326	2.004 \pm 0.574	2.255 \pm 1.237
Clutch wt./body wt. ratio	0.155	0.192	0.169
\bar{x} weight of one egg, g	0.319 \pm 0.078	0.443 \pm 0.039	0.517 \pm 0.122
Egg wt./body wt. ratio	0.039	0.043	0.039

and Ohmart (1977) could find no clear pattern of fat body cycling in *Callisaurus* females.

Evidence of multiple clutches was exhibited by both species. A 56-mm *Cophosaurus* captured 2 June contained three yolke follicles 3 mm in diameter and three corpora lutea 1 mm in diameter. Another specimen 60 mm s-v captured on 21 July contained three 3-mm follicles and three 1-mm corpora lutea. Similarly, a 69- and a 65-mm *Callisaurus* from Burro Creek captured on 2 June and 21 July respectively both contained 3-mm ovarian follicles undergoing vitellogenesis as well as oviducal eggs 15 mm in length. From Rock Valley a 78-mm *Callisaurus* captured 24 May contained six 3-mm follicles and seven 17-mm oviducal eggs with corresponding corpora lutea. Another specimen 84 mm s-v from 4 June contained seven 4-mm follicles and eight corpora lutea measuring 2 mm. In addition to the six sand lizards already mentioned, four *Cophosaurus* between the dates of 1 June and 24 June, one *Callisaurus* from Burro Creek on 21 July, and one from Rock Valley on 13 July contained 2-mm follicles initiating vitellogenesis as well as oviducal eggs and/or corpora lutea. Given a reproductive period of at least three months, multiple clutches were probably common in Burro Creek populations of both species and *Callisaurus* of Rock Valley in 1973. The large range of sizes exhibited by hatchling sand lizards of both species in September at Burro Creek also supports this conclusion (Table 3). Engeling (1972) found *Cophosaurus* to hatch from June through October, and Whitford and Creusere (1977) reported similar findings.

Most investigators of these lizards have considered them to produce multiple clutches, but the evidence is more conclusive for *Cophosaurus* (Ballinger et al. 1972, En-

geling 1972, Howland 1984, Johnson 1960, Vitt 1977) than for *Callisaurus* (Pianka and Parker 1972, Tanner and Krogh 1975). Vitt (1977) and this paper, however, present strong evidence for multiple clutches in *Callisaurus*.

Tinkle (1969, Tinkle et al. 1970) has elucidated the concept of reproductive effort and its adaptive and evolutionary significance as it applies to lizard populations. To facilitate these considerations, we have also tabulated reproductive data (Table 4) based solely on females carrying oviducal eggs. In comparison with published accounts, the Burro Creek populations of *Cophosaurus* and *Callisaurus* and the Rock Valley *Callisaurus* exhibited egg weight/body weight ratios of 0.039, 0.043, and 0.039 respectively that are much lower than 0.056 and 0.058 for *Cophosaurus* and *Callisaurus* presented by Vitt (1977). The clutch weight/body weight ratio of 15.5% for *Cophosaurus* is also much lower than the 21.8% presented by Ballinger et al. (1972) for a population of *Cophosaurus* in Texas. In further contrast to Ballinger et al. (1972), we did not find the mean weight of eggs of *Cophosaurus* to be smaller in smaller females. In fact, we generally found the opposite to be true, but not significantly so. The smallest mean oviducal egg weights of 0.171, 0.197, 0.242, and 0.287 were associated with females having s-v lengths of 64, 64, 59, and 63 mm respectively, and 64 mm was the largest s-v length for a female of this species at Burro Creek. All four of these small mean egg weights were associated with large clutches of five eggs each. The largest mean egg weight of 0.409, however, was obtained from a 62-mm female, also with five eggs.

MALE REPRODUCTIVE CYCLE.—Table 5 shows testicular measurements and fat body

TABLE 5. Testicular size (mm) and fat body weight for male sand lizards ≥ 60 mm s-v. Day is mean date of collection.

Day and month	s-v range in mm (mean)	N	\bar{x} testes length \times width (mm)	\bar{x} testes weight (S.D.) (g)	\bar{x} fat body weight (S.D.) (g)
<i>Cophosaurus</i> (Burro Creek)					
28 Apr	67-71(68.7)	3	6.3 \times 4.3	.082 (\pm .020)	.054 (\pm .012)
1 Jun	60-74(67.7)	20	6.5 \times 5.2	.090 (\pm .023)	.059 (\pm .048)
23 Jun	60-70(66.2)	6	6.3 \times 4.5	.077 (\pm .021)	.014 (\pm .009)
21 Jul	62-77(68.3)	13	6.4 \times 5.1	.091 (\pm .024)	.027 (\pm .044)
8 Sep	61-70(65.4)	11	3.0 \times 2.0	.003 (\pm .002)	.109 (\pm .108)
6 Apr	62-69(65.0)	4	5.5 \times 4.3	.050 (\pm .013)	.033 (\pm .023)
<i>Callisaurus</i> (Burro Creek)					
3 Mar	65-75(71.3)	4	4.0 \times 3.0	.038 (\pm .033)	.004 (\pm .005)
7 Apr	74-76(75.0)	2	6.0 \times 4.5	.102 (\pm .036)	.007 (\pm .009)
28 Apr	66-81(74.5)	6	7.7 \times 6.2	.175 (\pm .046)	.057 (\pm .061)
1 Jun	63-84(76.7)	6	7.0 \times 5.2	.147 (\pm .046)	.027 (\pm .048)
23 Jun	62-83(75.7)	7	6.9 \times 5.3	.105 (\pm .039)	.067 (\pm .054)
21 Jul	74-84(77.8)	12	7.4 \times 5.3	.118 (\pm .033)	.031 (\pm .048)
8 Sep	70-75(72.8)	5	3.2 \times 2.0	.003 (\pm .002)	.092 (\pm .075)
6 Apr	61-82(75.0)	4	5.5 \times 4.0	.079 (\pm .059)	.035 (\pm .027)
<i>Callisaurus</i> (Rock Valley)					
27 Apr	64-87(79.6)	10	7.2 \times 5.5	.159 (\pm .086)	.132 (\pm .198)
6 Jun	77-89(83.1)	8	8.6 \times 6.3	.256 (\pm .074)	.210 (\pm .114)
8 Jul	68-94(82.6)	16	6.3 \times 4.9	.139 (\pm .167)	.273 (\pm .247)
25 Jul	79-90(85.3)	6	5.8 \times 3.8	.057 (\pm .016)	.514 (\pm .249)
13 Sep	77	1	5 \times 2	.023	1.076

weights of male lizards from Burro Creek and Rock Valley. Minimum testicular measurements were obtained during the month of September in all populations. Maximum testicular measurements were obtained for *Cophosaurus* on 1 June and 21 July, for *Callisaurus* at Burro Creek on 28 April, and for *Callisaurus* from Rock Valley during early June. Maximum mean fat body sizes were obtained in the month of September for all populations. Minimal measurements were obtained for *Cophosaurus* on 23 June, in March and April for *Callisaurus* from Burro Creek, and in April for *Callisaurus* from Rock Valley; however, as with females, fat bodies of males from Rock Valley were enlarged throughout 1973.

The male reproductive cycles of both lizards have been well studied (Shrank and Ballinger 1973, Pianka and Parker 1972, Tanner and Krogh 1975, Vitt and Ohmart 1977), and for the most part our results are comparable. However, the maintenance of enlarged fat bodies throughout the reproductive season by *Callisaurus* at Rock Valley is unusual and probably reflects an unusually good food supply at that locality for that year.

FOOD HABITS

We have compared food habits of *Cophosaurus texanus* and *Callisaurus draconoides* from Burro Creek at two levels. First, we compared the orders of organisms eaten during the entire sampling period (Figs. 1 and 2). Secondly, we compared orders of organisms consumed on a monthly basis (Table 6).

Upon comparison of the pie diagrams, we find that insects comprised over 90% of the diet for both species. However, the quantities of each order consumed by each species varied considerably. Almost 50% of the diet of *Callisaurus* consisted of Orthoptera and Lepidoptera, whereas *Cophosaurus* consumed 18% Orthoptera, about 16% Hymenoptera, and only 10% Lepidoptera and also displayed considerably more dependency upon Coleoptera and Araneida than did *Callisaurus*. Niche overlap, based on these data and calculated using the formula of Pianka (1973, 1974), is high at 0.88.

Our findings at the familial level (unpublished data) indicate that niche overlap for these resources in reality may not be this high. Although both species were observed in

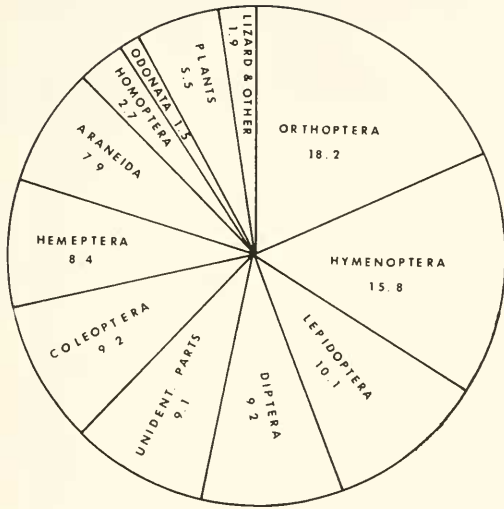


Fig. 1. Food habits of *Cophosaurus texanus* during 1973 and 1974, indicating percent volume of each category.

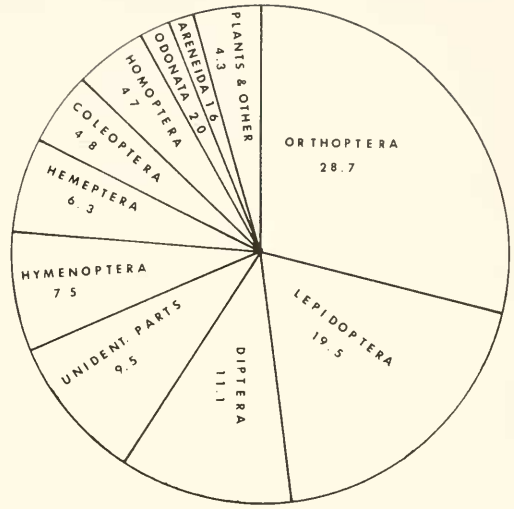


Fig. 2. Food habits of *Callisaurus draconoides* during 1973 and 1974, indicating percent volume of each category.

the riparian habitat (see ACTIVITY), *Cophosaurus* tended to feed closer to the stream than did *Callisaurus*. For example, in the Orthoptera we find that both species ate acridids, but *Cophosaurus* consumed far fewer acridids than did *Callisaurus*. Instead, *Cophosaurus* was found to feed heavily upon tetrigids and tridaetylids. In the Coleoptera we saw a similar trend, for of the two lizards only *Cophosaurus* consumed hydrophilids, omophronids, and psephenids. This trend was not as obvious in other families because they are not characterized by their occurrence in limnological habitats. This may also explain the greater volume of both Hymenoptera and Araneae in *Cophosaurus*, for there was probably a greater diversity and abundance of members of both these groups in the riparian habitat. Therefore, it is probable that *Callisaurus* feeds in the more xeric areas of the riparian habitat as indicated by the greater occurrence of acridids, lygaeids, and formicids.

During the late summer and early spring when hatchling lizards were abundant, we found that *Cophosaurus* occasionally supplemented their diet with vertebrate prey, particularly *Urosaurus ornatus*. No vertebrates were found in the stomachs of *Callisaurus*. Table 6 indicates that the diets of these two lizards are highly variable, and they are probably greatly influenced by blooms, hatches, and phenology as it relates to populations of

appropriately sized and edible insects. Throughout the activity season, however, Orthoptera seemed to constitute the primary food source of both species.

Engeling (1972) found that *Cophosaurus* most frequently ate orthopterans, hemipterans, coleopterans, and araneans. Pianka and Parker (1972) found *Callisaurus* to feed primarily on orthopterans and coleopterans in the U.S. and insect larvae and hymenopterans in Sonora, Mexico. Vitt and Ohmart (1975) found *Callisaurus* to primarily feed on orthopterans, and to a small extent (<1%) on small lizards. Tanner and Krogh (1975) and Kay et al. (1970) found *Callisaurus* to primarily feed upon hymenopterans and dipterans respectively. Pack (1923) found 10% of the food items consisted of vegetable matter, and 89% consisted of insects, with hymenopterans, lepidopterous larvae, neuropterans, hemipterans, and coleopterans represented in that order.

ACTIVITY

HABITAT PREFERENCE.—The plant association in which the lizards were first encountered gives an indication as to which habitat was preferred at Burro Creek. Table 7 indicates that *Cophosaurus* was primarily found in the riparian habitat (77.9%) and secondarily in the arroyos (14.2%), being usually re-

TABLE 6. Food habits of *Cophosaurus texanus* (*Coph.*) and *Callisaurus draconoides* (*Call.*) for 1973 and 1974 at Burro Creek, Mohave County, Arizona, indicating the percent volume of each category.

Taxon	March 1973		April 7, 1973		April 28, 1973		June 1, 1973		June 23, 1973	
	<i>Call.</i>		<i>Coph.</i>	<i>Call.</i>	<i>Coph.</i>	<i>Call.</i>	<i>Coph.</i>	<i>Call.</i>	<i>Coph.</i>	<i>Call.</i>
ARACHNIDA										
Araneida	5.7	—	2.1	—	1.3	7.5	2.2	11.2	1.7	
INSECTA										
Thysanura	—	—	—	—	—	0.2	—	—	—	
Odonata	—	—	—	—	—	—	—	—	—	
Orthoptera	0.4	—	—	—	21.4	25.8	4.7	22.0	32.8	42.4
Isoptera	—	—	—	—	—	—	—	—	—	—
Hemiptera	2.1	—	1.6	—	4.4	7.7	18.6	4.3	7.0	
Homoptera	2.1	—	—	—	—	0.6	0.4	0.7	2.1	
Neuroptera	—	—	—	—	4.3	0.7	1.3	0.8	—	0.6
Coleoptera	2.1	—	2.1	—	—	0.4	9.3	2.8	10.7	2.5
Lepidoptera	38.9	—	46.6	—	28.6	44.7	11.5	16.4	24.9	0.9
Diptera	28.2	—	34.1	—	—	14.2	15.4	12.0	2.6	2.5
Hymenoptera	5.4	—	6.8	—	42.9	2.2	31.2	13.6	1.2	10.9
Unidentified parts	7.1	—	6.2	—	2.9	6.0	5.9	6.8	7.8	28.8
ISOPODA										
	—	—	—	—	—	—	2.4	—	—	
PLANT MATERIAL										
	7.9	—	16.7	0.6	—	—	4.7	2.0	3.8	0.9
LIZARD (skin, parts)										
	—	—	—	—	—	—	—	—	—	—

stricted to the edges. *Callisaurus*, on the other hand, preferred the arroyos (57%), which have the largest expanses of open sandy spaces; secondarily they utilized the riparian association (40.7%).

The soil/substrate type in the riparian association is sand interspersed with numerous boulders, and this substrate was preferred by *Cophosaurus* 69.0% of the time. *Callisaurus* prefers the more open sandy areas and was taken on such substrate 72.0% of the time.

Niche overlap calculated by the formula of Pianka (1973, 1974) is higher based on habitat preference (0.71) than on the microhabitat determination of soil/substrate type (0.57). Therefore spatial partitioning is greatest at the level of the microhabitat, with *Cophosaurus* being characterized as more saxicolous than *Callisaurus*. Similar preferences have also been observed by Clarke (1965) and Engeling (1972), who noted the preferred habitat of *Cophosaurus* was dry creek beds with a preponderance of flat-surfaced limestone and sandstone. Pianka and Parker (1972) and Tanner and Krogh (1975) noted that *Callisaurus* preferred open areas of desert flats and valleys. Whitford and Creusere (1977) found *Cophosaurus* to be a permanent resident of the arroyo-shrub association and a transient resident in open *Larrea*.

TIME OF ACTIVITY.—Table 8 shows the frequency of collection of *Cophosaurus* and *Cal-*

lisaurus at Burro Creek during 12 daily time intervals. *Cophosaurus* was most active between 0900 and 1300 hr with another period of activity initiated after 1700 hr. *Callisaurus* probably initiated activity a little earlier than *Cophosaurus* and decreased activity about 1200 hr. Also, they exhibited a less-pronounced peak of evening activity. Temporal niche overlap calculated by the formula of Pianka (1973, 1974) is high at 0.86.

Engeling (1972) found *Cophosaurus* most active in the afternoon, but some activity was observed at nearly all hours of the day between 0919 and 1948 hr. Pianka and Parker (1972) found *Callisaurus* active as early as 0730 and suggested bimodal diel activity. Tanner and Krogh (1975) found *Callisaurus* rather heat tolerant, seldom active before 0800, and considered them to remain active throughout the heat of the day. Kay (1970), who has probably done the most extensive activity study, found *Callisaurus* to be active throughout the day, but showing weak bimodality through the summer.

TEMPERATURE RELATIONSHIPS.—The mean body temperature of *Cophosaurus texanus* was 38.5 C (± 1.5 , $n = 73$) and of *Callisaurus draconoides* was 38.2 C (± 2.4 , $n = 96$). The mean surface soil temperature and air temperature within 2 cm of the soil at the point of capture were 42.0 C (± 5.1 , $n = 69$) and 36.0 C (± 4.4 , $n = 68$) for *Cophosaurus*, and 40.5 C

Table 6 continued.

July 21, 1973		Sept. 8, 1973		April 7, 1974	
<i>Coph.</i>	<i>Call.</i>	<i>Coph.</i>	<i>Call.</i>	<i>Coph.</i>	<i>Call.</i>
14.3	0.3	1.6	0.4	3.3	0.8
—	—	—	—	—	—
—	—	6.3	16.8	4.0	—
28.2	54.6	39.2	44.8	5.7	1.1
—	—	1.1	3.2	—	—
1.9	1.6	2.9	7.4	31.6	11.4
11.1	21.8	—	0.6	—	1.2
—	—	—	—	—	—
5.6	8.4	16.5	7.1	7.5	18.4
4.3	3.1	2.5	1.1	9.8	4.1
5.1	0.7	3.6	1.1	4.0	4.5
7.6	2.2	4.0	9.9	12.9	17.6
12.7	6.9	13.4	7.1	9.7	4.5
—	—	—	—	—	—
4.1	—	5.4	0.4	10.9	36.3
5.1	—	3.4	—	—	—

(± 7.8 , $n = 90$) and 35.8 C (± 5.0 , $n = 65$) for *Callisaurus* respectively. There are no differences in these respective pairs of means between *Cophosaurus* and *Callisaurus* at the .05 level of significance.

Clarke (1965) found the mean body temperature of *Cophosaurus* to be 38.3 C and 39.2 C for *Callisaurus* and related this difference to geographic distribution, with *Callisaurus* generally living in the warmer locales. Most other studies have also found the mean or median body temperature for *Callisaurus* to be 39.1 C or slightly higher (Packard and Packard 1970, Pianka and Parker 1972, Tanner and Krogh 1975). We conclude from our data that there is virtually no difference in the temperature responses of the two species when exposed to the same or similar ambient temperatures as with the two populations at Burro Creek. Muth (1977a, 1977b) has correlated and analyzed body temperatures and associated posturing in *Callisaurus*.

SUMMARY AND CONCLUSIONS

From this study a number of conclusions can be drawn concerning the biology of *Cophosaurus* and *Callisaurus* at Burro Creek and *Callisaurus* at Rock Valley. Sex ratios of adult *Cophosaurus* were unequal in our samples, with a larger number of males being

present. This, however, may have been due to sampling error and the fact that males are more obvious. Sex ratios of adult *Callisaurus* from both Burro Creek and Rock Valley were approximately equal, but in samples of juveniles, females outnumbered males.

Most males and females of both species became reproductively mature after their first hibernation. Reproductive seasons last from April through August, and mean clutch sizes of 3.55, 4.25, and 5.07 were determined for *Cophosaurus* and *Callisaurus* from Burro Creek and Rock Valley respectively. Multiple clutches were probably common among individuals of both species, but evidence for this at Rock Valley was found only in larger and presumably older adults. Also, the reproductive season is probably terminated two to three weeks earlier in this northern population.

Mean egg size of both species of lizards and clutch size/body weight ratios of *Cophosaurus* were determined to be smaller than reported previously from other populations (Vitt 1977, Ballinger et al. 1972).

The male reproductive cycles of both species were found to be similar to those previously reported. However, corpora adiposa of both male and female *Callisaurus* from Rock Valley remained relatively large throughout the summer, presumably because of abundant food at that locality in 1973.

The food habits of both *Cophosaurus* and *Callisaurus* at Burro Creek are similar, but they are probably greatly influenced by sporadic and episodic availability. Both lizards are highly insectivorous with Orthoptera being the staple food during the summer months.

Differences between preference of macrohabitat and microhabitat were observed, *Callisaurus* preferring sandy open areas and *Cophosaurus* preferring the presence of some rocks and boulders. Both lizards maintained similar daily activity patterns. *Callisaurus* may initiate activity earlier in the day than *Cophosaurus*, but some *Cophosaurus* tend to remain active throughout the day. *Cophosaurus* has a more pronounced activity period in the evening than was observed for *Callisaurus*. Temperature relationships are very similar for the two species.

Niche overlap for the two populations at Burro Creek was calculated at 0.71, 0.57, 0.86, and 0.88 at the levels of macrohabitat,

TABLE 7. Habitat preferences of *Cophosaurus* and *Callisaurus* at Burro Creek, based upon plant associations and soil type. Figures are frequency of encounters in percent.

Plant association	<i>Cophosaurus</i>	<i>Callisaurus</i>
Riparian	77.9	40.5
Arroyo	14.2	56.9
Acacia	—	1.7
Paloverde-Sahuaró	7.9	0.9
Totals	100.0	100.0
Soil/substrate type		
Sand	24.8	72.0
Gravel	6.2	8.8
Boulders	69.0	19.2
Totals	100.0	100.0

microhabitat, time of activity, and food habits respectively. The values of microhabitat and temporal overlap are very similar to the mean values for North American lizards calculated by Pianka (1973) at 0.55 and 0.86 respectively. But niche overlap at the trophic level is much higher at Burro Creek at 0.88 compared to Pianka's mean value of 0.49. It is probable that the productive environs associated with the riparian habitat in an otherwise desert community are responsible for the coexistence of these two similar sand lizards at Burro Creek.

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TABLE 8. Frequency of collections of *Cophosaurus* and *Callisaurus* at 12 daily time intervals at Burro Creek.

Time interval	<i>Cophosaurus</i>		<i>Callisaurus</i>	
	N	Percent frequency	N	Percent frequency
0700-0759	0	0.0	3	2.3
0800-0859	4	3.5	10	7.8
0900-0959	13	11.3	39	30.2
1000-1059	29	25.2	34	26.4
1100-1159	22	19.1	20	15.5
1200-1259	18	15.7	10	7.8
1300-1359	5	4.3	6	4.7
1400-1459	2	1.7	0	0.0
1500-1559	3	2.6	0	0.0
1600-1659	2	1.7	0	0.0
1700-1759	10	8.7	1	0.8
1800-1859	7	6.1	6	4.7
Totals	115	99.9	129	100.2

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